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Bats of the La Gamba region, Esquinas rainforest, Costa Rica: species diversity, guild structure and niche segregation

Murciélagos de la región de La Gamba, bosque lluvioso Esquinas, Costa Rica: diversidad específica, estructura gremial y segregación de nichos

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Abstract: The Piedras Blancas National Park in south-west Costa Rica harbours some of the most species-rich habitats in Central America. We give a first overview of its bat fauna and investigate differences of species diversity and bat community structures between habitats with different levels of disturbance for a representative sub-area at the eastern edge of the park. With 49 species, the small 6 km^2 investigation area around La Gamba exhibits a very high bat diversity including many species considered rare or uncommon in Costa Rica. A total of 1702 bats was captured in mist nets over 59 nights from January to March 1997 and 2004. Capture rates were higher at gallery woodlands and at secondary forest margins than at primary rainforest sites, but the latter showed higher species numbers and a more balanced dominance structure. Primary habitats also had the highest number of foraging guilds and especially gleaning insectivores and nectarivores were mostly found in mature forests. Understorey gleaning frugivores (*Carollia* spp.) and a few aerial insectivores, on the other hand, made up a high proportion of total captures in the cultivated landscape. There, gallery woodlands, live fences and shaded plantations proved to be important flyways and foraging places for a surprisingly diverse bat fauna (30 species recorded). Differences in average capture heights at ground level mist nets indicate fine tuned spatial niche segregation between some aerial insectivores, but only to a low extent for members of frugivorous guilds.

Key words: Costa Rica, Microchiroptera, alpha diversity, habitat disruption, foraging guilds, corridors, countryside ecology.

Resumen: El Parque Nacional Piedras Blancas en el suroeste de Costa Rica alberga algunas de las zonas de vida más ricas en especies de Centroamérica. Damos una primera visión general de su quiropterofauna e investigamos diferencias en diversidad de especies y estructura de la comunidad de murciélagos entre hábitats con diferentes grados de perturbación, para un área representativa del borde este del parque. Con 49 especies, el área pequeña de investigación de 6 km² alrededor de La Gamba tiene una alta diversidad de murciélagos con muchas especies hasta ahora reportadas como raras o poco comunes en Costa Rica. Los murciélagos fueron capturados en 59 noches de enero a marzo de 1997 y 2004, con un total de 1702 capturas. Las tasas de captura fueron más altas en bosque de galería y las márgenes del bosque secundario que en los sitios de bosque primario, pero estos últimos mostraron números mayores de especies y una estructura de dominio más balanceada. Los hábitats primarios también tuvieron el mayor número de gremios alimentarios. Especialmente los insectívoros recolectores y los nectarívoros se encontraron mayormente en bosques maduros. De otra parte, los frugívoros recolectores del sotobosque (*Carollia* spp.) y algunos insectívoros aéreos representaron una alta proporción de las capturas totales en el paisaje cultivado. Ahí, los bosques de galería, cercas vivas y plantíos con sombra emergieron como importantes rutas de vuelo y lugares de alimentación para una fauna de murciélagos sorprendentemente diversa (30 especies registradas). Diferencias en la altura promedio de capturas con redes a nivel del suelo indican una segregación fina de nichos espaciales entre algunos insectívoros aéreos, pero solo en menor grado para los miembros de los gremios de frugívoros.

Palabras clave: Costa Rica, Microquiroptera, diversidad alfa, discontinuidad de hábitat, gremios alimentarios, corredores, ecología de campo.

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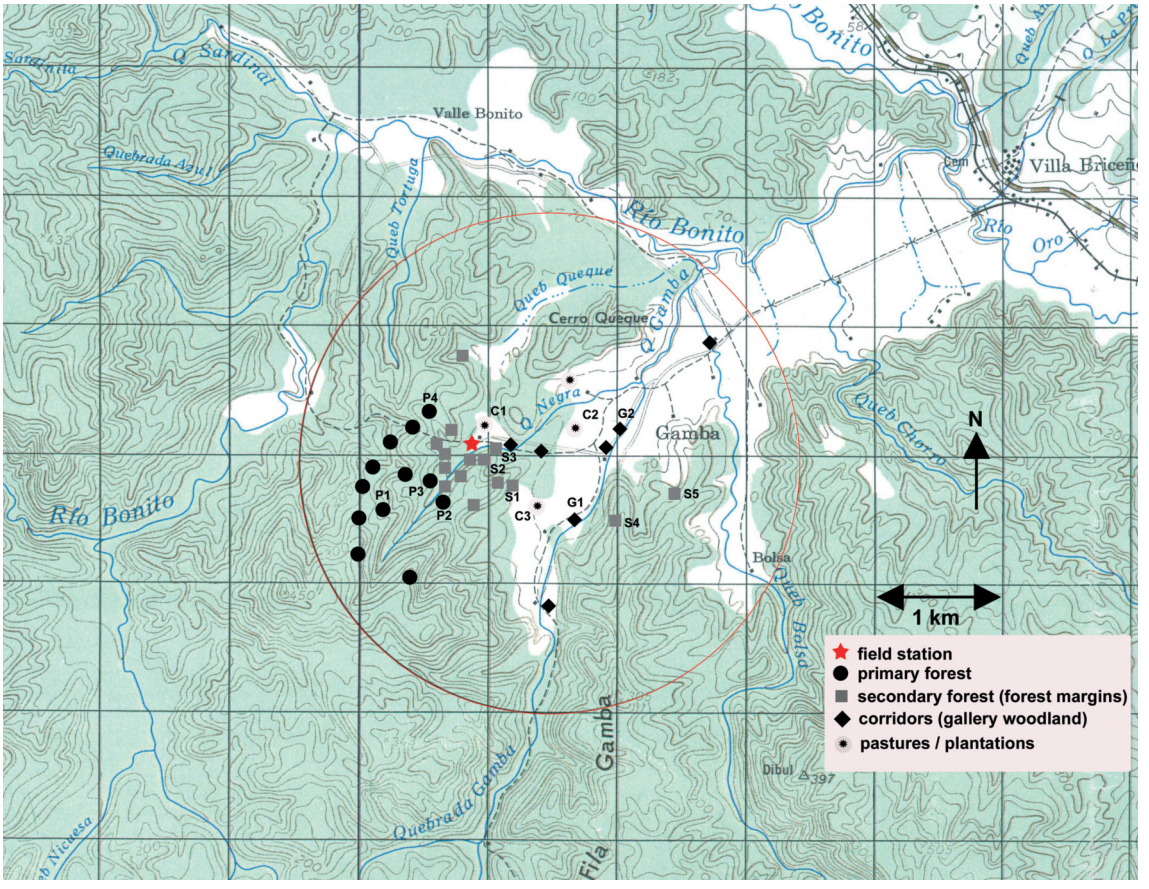

Fig. 1: Investigation area around La Gamba, near Golfito, SW Costa Rica, with sample sites at different habitats. P1-4, S1-4, C1-3, G1-2 = sites sampled 2004; symbols without number = sites sampled 1997. Five pasture-sites sampled in the year 1997 are within a diameter of 150 m of C1 and therefore not plotted separately. Map source: Instituto Geografico de Costa Rica, E-736, Edicio´n 1-IGCR 1964; Hoja 3542-I, Piedras Blancas.

Introduction

Among mammals, bats are unsurpassed in ecological diversity, and in tropical forests more than 100 species may coexist (e.g. FINDLEY 1976, HELLER & VOLLETH 1995, VOSS & EMMONS 1996). In tropical ecosystems, bats play indispensable roles in dispersing large quantities of seeds, pollinating flowers and controlling insect populations (e.g. KALKO & HANDLEY 2001). Accordingly, a large number of papers has been published not only on the biology and ecology of tropical bat species, but also on alpha-diversity and guild structures of bat communities in neotropical forests including many Central American locations (e.g. HUMPHREY et al. 1983, ARITA 1997, ESTRADA & COATES ESTRADA 2001, FENTON et al. 2001, GIANNINI & KALKO 2005, STONER 2005, MEDINA et al. 2007).

Nevertheless, habitat loss and degradation of tropical regions goes on undamped with, for example, an estimated annual loss of 4 million ha of forest cover in Latin America alone (GROOMBRIDGE & JENKINS 2002). Thus in recent years, an increasing number of contributions has also dealt with the impact of forest destruction and fragmentation on neotropical bat faunas (e.g. COSSON et al. 1999, CUARON 2000, MEDELLÍN et al. 2000, QUESADA et al. 2003, CLARKE et al. 2005, PETERS et al. 2006), a problem which is also present in the focus area of this book.

In Costa Rica itself, bat research has a long tradition. Besides a number of more specialised studies on the ecology of single species (e.g. CASEBEER et al. 1963, FENTON et al. 1993, WOHLGENANT 1994, STONER 1997, 2001) and of local bat communities (e.g. LAVAL & FITCH 1977, DINERSTEIN 1986, TIMM 1994, RIBA-HERNÁNDEZ 1996, TSCHAPKA 2004, STONER 2005), some broader overviews about the bat fauna of the entire country (GARDNER et al. 1970, RODRIGUEZ & CHINCHILLA 1996, RODRIGUEZ & WILSON 1999, LAVAL & RODRIGUEZ 2002) have been published, including identification guides (REID 1997, TIMM & LAVAL 1998).

Very little information, however, is available about the status and conservation of bats in the south-western part of the country (i.e. the Golfo Dulce region). As this area hosts one of the last conserved lowland rainforests on the Pacific coast of Central America, data about general habitat requirements, local species richness and regional distribution patterns are urgently needed to evaluate and monitor the results of rapid changes in natural and environmental conditions for the bat fauna of this hot spot of biodiversity.

In this paper we therefore aim to (1) give a first overview about the bat fauna in the area of the Piedras Blancas National Park (Esquinas Rainforest), and (2) assess differences in bat species assemblages (species diversity, relative species abundance and foraging guild

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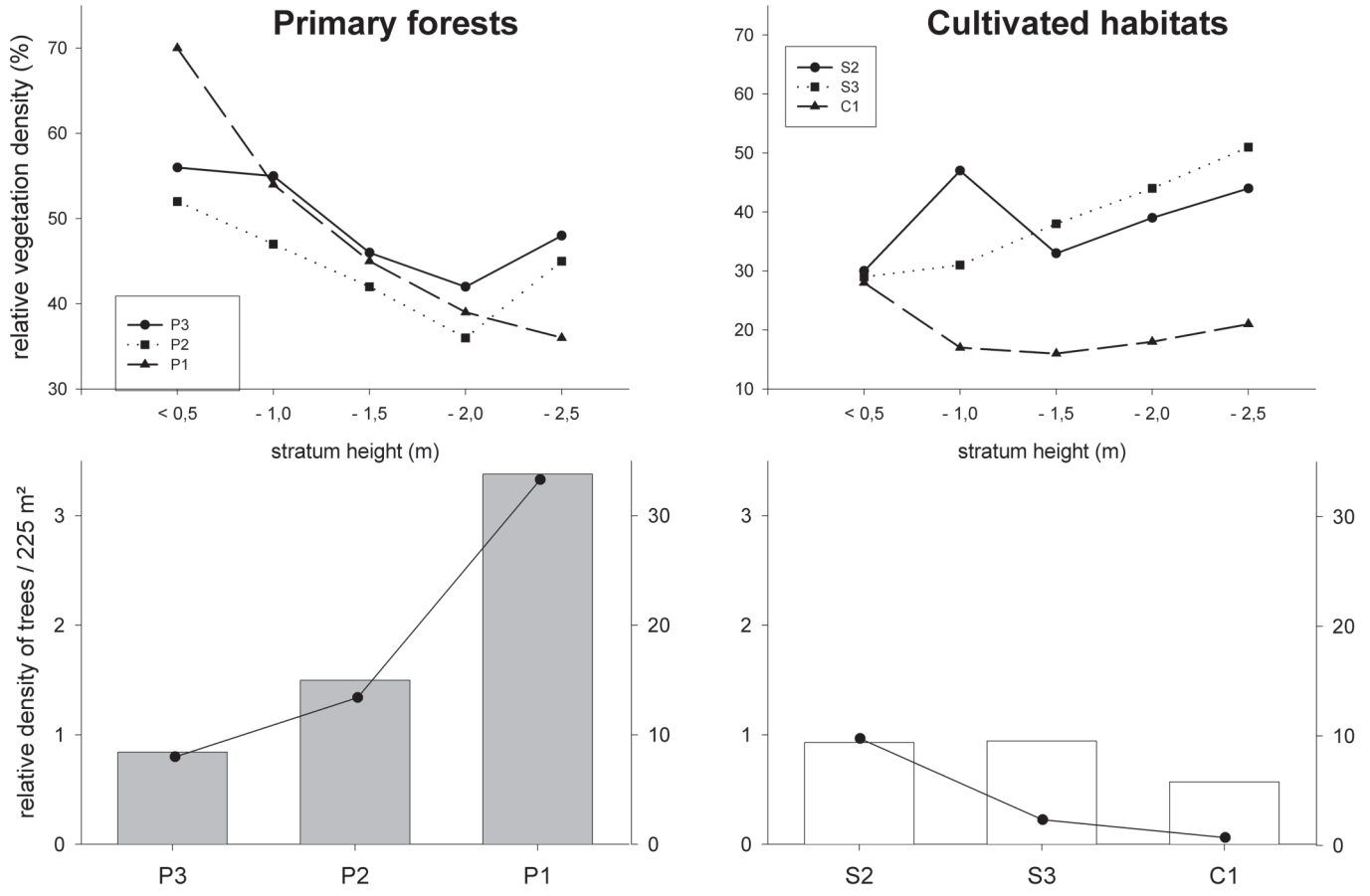

Fig. 2: Differences in vegetation structures between three primary and three disturbed habitats in and around the Esquinas Forest. Tree densities are plotted separately for trees with a d.b.h. < 35 cm (lines; right axis) and for mature trees (d.b.h. > 35 cm; bars, left axis). Site numbers and methods see Fig. 1 and text.

structures) between habitats differing in human impact for a small but representative area of the park. For this comparison, we use field data sampled in the course of the research project "Mammals of the Costa Rican Rainforest of the Austrians" (LANDMANN et al. 2003) together with extensive data collected in an earlier study by WEINBEER (cf. WEINBEER & STONER 1997/99) from a "gradient of disturbance". This gradient covers sites with pristine rainforest, disturbed patches at forest edges (degraded primary and secondary forest), as well as intensely used semi-open to open landscapes outside the national park (gallery woodland along streams, plantations, pastures). In addition, for a subset of species, we test if capture heights at ground level mist nets might serve as a raw indicator of niche segregation between species within a given foraging guild.

Materials and Methods

Investigation area, study sites

Our research has been based on the La Gamba Field Station (8°42´N, 83°12´W) at the eastern edge of the Piedras Blancas National Park (also called Esquinas forest or "Rainforest of the Austrians") in the south-western corner of Costa Rica (Golfo Dulce region). Details about the climate, landscape and vegetation of the area are given in WEISSENHOFER & HUBER 2001, WEISSENHOFER et al. 2001, and other contributions within this book.

Our main investigation area covers an area of approximately 6 km^2 within a diameter of 2 km around the La Gamba biological field station (Fig. 1). Additional data stem from other places, especially from one roosting site (cave) about 3 km north-east of the border of the national park. Details about vegetation structures and floral composition of the different habitats in the sampling area (including descriptions of most of our sample sites) are given in HUBER 2005, WEISSENHOFER 2005 and WEISSENHOFER et al. 2001 (with further references). Within our main investigation area, 29 mist net sites in 1997 and 14 sampling sites in 2004 were selected (Fig. 1). These sites can be assigned to four different main habitat types. As all sites of each type are situated close together and as detailed habitat measurements were carried out only 2004 we focus on a structural descriptions of our 2004 sites (Fig. 2).

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Table 1: Sampling effort, sampling efficiency, number of bats captured and number of species identified in each habitat (site) sampled. Data are given for each single site sampled in 2004 and summarised for 8 primary forest (P), 10 secondary forest (S), 6 cultivated land (C) and 5 corridor sites (gallery forests: G) sampled by Weinbeer 1997 (= W 1997). Capture rates are lower for 1997 samples mainly because entire night sampling included low activity periods of bats then.

Site	P1	P2	P3	P4	S1	S2	S3	S4	S5	C1	C2	C3	G2	G1
Sample nights 2004	2	2	2	1	1	2	2	2	2	2	2	2	1	1
W 1997		11					13				9		5	
Net h	40	40	40	20	20	28	28	20	20	40	40	40	15	15
W 1997		389					389				389		167	
Species 2004	7	12	13	10	12	14	10	4	14	12	9	10	16	14
		(25 species 2004)					(31)				(15)		(19)	
W 1997		30					28				7		22	
Individuals 2004	74	49	43	50	66	136	65	17	49	39	24	30	72	65
W 1997		264					442				17		199	
Capt.-rate* 2004	4.36	2.89	2.53	5.90	7.78	12.2	8.12	2.00	5.78	2.30	2.83	3.53	11.3	12.3
W 1997		2.26					3.79				1.46 **		3.98	

* Capture rate = bat individuals/m^2/h x 10^{-2} , ** = bat individuals/m^2/h x 10^{-3}

Primary forest within the national park (8 sites 1997, 4 sites 2004)

Our primary forest sites (altitudes between 80 and 250 m above sea level) belong to three main types of rainforest: ridge forest (most sites 1997, P1, 2004,), slope forest (P2, P4: 2004) and gorge forest (one site 1997, P3, 2004). The floristic composition and vegetation at and around these sites are described in detail in HUBER 2005 and WEISSENHOFER 2005. The relative canopy cover as derived from our own measurements in the year 2004 varied from 77% (P3) to 87% (P1) and the relative horizontal vegetation cover (density) in the understorey (< 1 m) from 50% (P2) to 60% (P1; further differences see also Fig 2.).

Forest margins, secondary forests (10 sites 1997, 5 sites 2004)

This habitat type comprises a heterogeneous sample of tree-dominated sites with different levels of disturbance, alteration and of isolation from primary habitats. All sites were located at altitudes from 75 to 150 m. All ten sites sampled 1997 by Weinbeer were within 250 m of the field station (see Fig. 1) and consisted primarily of shrubs and small trees (d.b.h. < 20 cm). Our 2004 sample sites nearby included: (S1) a forest edge with remains of primary forest but including clearings with reedy vegetation and high shrub densities and with very low canopy cover (31%), (S2) an abandoned cocoa plantation (Fig. 2, Photo Fig. 4c) close to the field station in the state of regrowth (some single tall trees; canopy cover > 80%; high vegetation density in the lower strata see Fig. 2), and (S3) a semi open, park-like area around an abandoned finca (= old field station) at the edge of the forest. This area included a small pond and a tiny banana plantation, and the density of small to medium-sized trees was still high (canopy cover 63%, see Fig. 2). Whereas the above 13 sites were in close vicinity to the biological station at the border of the national park (i.e. close to primary forest, see Fig. 1), two additional sites sampled only in 2004 were located 1.3 to 1.7 km from the biological station (national park border) across the open (cultivated) valley of the Rio Gamba. Both sites (S4 & S5) were situated at forest edges near the valley floor in the foot hills of the Fila Gamba, a ridge (up to 305 m asl.) covered with comparatively dense secondary forests (canopy cover at the sampling sites: S4: 67%; S5: 81%).

In general, most forest margins (as well as gallery woodland, see below) in our sample are characterised by high densities of important food plants for frugivorous bat species (e.g. *Carollia* & *Artibeus* spp.) like *Vismia baccifer* (Clusiaceae), *Piper hispidum* (Piperaceae) and *Solanum* spp. (Solanaceae).

Cultivated land (6 sites 1997, 3 sites 2004)

This habitat type comprises open to semi-open disturbed landscapes outside the national park in the floodplains of the Quebrada Negra and Quebrada Gamba valleys (70-80 m asl). The investigated cattle pastures differed in the numbers and density of residual trees and shrubby vegetation (mostly small *Cecropia* stands, some shrubs of Mimosaceae, Onagraceae). Site C1 was close (50-250 m distance) to the (disturbed) edge of the forest, and was only lightly grazed. Two habitat subsets (more open pasture and pasture near forest edge) with comparatively high canopy cover (19 and 57% respectively) were sampled in 2004 (see Fig. 2, Photo Fig. 3d). Mainly within the area of this pasture, Weinbeer also collected bat data at six single mist-net sites in 1997. Site C2 in the centre of the La Gamba valley had only scattered small trees and shrubs along a small creek and at its margins, and was intensively grazed (high densities of cattle). Some cattle grazing also took place in our third "cultivated land" sampling site (C3), an old oil palm plantation in the middle of the open valley of the Rio Gamba (distance to forest edges

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> 300 m). At this site, oil palms covered about 57% of the area (relative canopy cover) but in the open spaces along three small creeks, grasses and reeds vegetation were dominant.

Gallery forest and other corridor habitats (5 sites in 1997, 2 sites in 2004)

Bat data from five corridor sites (Fig. 1) are available from the 1997 investigations. Three corridors were recognised as stands of trees (live fences) between pastures consisting mainly of *Erythrina costaricensis* (Fabaceae) and *Gmelina arborea* (Verbenaceae). One corridor was close to a creek (Quebrada Bolsa) crossing a pasture. Its edges were covered with bushes and small trees. The fifth corridor was along the border of a cattle pasture, consisting of fences, finca house walls and a few trees. Corridors usually connected forested areas that were located 100 m to a few kilometres away from each other. Nets were set perpendicular to the direction of the corridor in order to capture bats flying along the line.

In 2004 we investigated two additional forested corridor sites (70 m asl.) along the Quebrada Gamba, crossing pastures and other open cultivated land (Fig. 1). The width and structure of the gallery woodland along the small "La Gamba river" varies within the valley (from single tree stands to forests with 20-50 m width), but overall the trees and shrubs along the river form an important undisrupted corridor in the landscape. At both sites, trails, solitary farm houses (fincas) and small strips of plantations (banana, oil palm) were located near the river. The gallery forest at site G1 (ca. 1 km south of site G2) was less diverse (young afforestation with low shrub density in the open understorey; canopy cover approx. 56%) than at site G2 (a good mixture of trees and tall shrubs and open spaces; canopy cover approx. 42%). Food plants for frugivorous bats were abundant along the rivers (see above).

Vegetation measurements, habitat attributes

We used a few simple, standardised methods to assess (measure) habitat features in order to characterise local conditions and to compare sites:

A value for canopy cover was derived from averaged estimates at 45 randomly chosen points within each study site. At each point we used a simple eye tube (diameter 10 cm, length 25 cm) to assess the percentage of visible air in the canopy. The mean horizontal vegetation cover (or density) in the understorey was assessed by using a 2.5 m tall strip board (five alternating red and white bands, 0.5 m wide) at 36 random points within each study site. At each point, we estimated the proportion of the bands remaining visible (or being covered by vegetation respectively) from approximately 7 m distance at 5 height classes (-0.5 m, -1 m, -1.5 m, -2 m, -2.5 m).

The vegetation cover or proportion of bare ground at the forest floor was estimated for 45 randomly selected 4 m² plots per site. Data about tree densities were collected using the "point centred quarter method" (MUELLER-DOMBOIS & ELLENBERG 1974) at 15 randomly chosen quadrants per study site.

As the above measurements took place only at some representative sites and only during the 2004 investigations, the data are only used here to give a better impression about structural differences of the main habitats and not used for further analysis of bat communities (Fig. 2).

Sampling of bats

Bats were captured in Japanese mist nets (36 mm mesh width) during 38 nights from 2 January to 26 March 1997 and during 21 nights between 17 January and 26 March 2004. Details about sampling effort and sampling efficiency in different habitats and sampling periods are given in Table 1.

For data collection in 1997, Weinbeer used three to five 12 m wide by 2.5 m tall nets. Nets were positioned in a line, in perpendicular positions to one another, with resulting total net-lanes of 50-70 m, and distances between nets of 5-20 m. Sampling was conducted 21 nights in January, 13 in February, and four in March. Habitats were changed for sampling approximately every night to minimise meteorological or lunar phase biases. Nets were opened from 17.30 h to 5.30 h for the first 21 nights, from 17.30 h to 0.30 h for the following 13 nights, and entire night sampling was again conducted for the last four nights. Nets were occasionally closed during this period due to heavy rain and mist netting time was interrupted. Mist net efforts (net hours) were equal for all habitats, except for the corridor habitat, where it was less than half (Table 1). Nets were monitored in 10 min intervals. Captured bats were identified to species (using the keys of TIMM & LAVAL, 1998 and HANDLEY, in press), sexed, weighed and measured directly at the sampling sites. Before release, bats were marked by cutting a small amount of hair on the back of the head in order to recognise them as recaptured.

Data collection took place in a similar way in 2004, but the following differences should be remarked. At each site one 6 m wide, two 8 m wide, and two 12 m wide and 3-4.5 m tall nets were opened at dusk for only 4 h (1730-2130 hrs), which corresponds to peak foraging times of most ground dwelling bats. At six sites (P1-P3, S2-S3, C1), sampling took place at two nights (period 1: 26.1-11.02; period 2: 15.02.-11.03), at the other sites only one night was sampled (13.3-20.3). For each individual bat captured, the capture height in the net was noticed (estimated to the nearest 10 cm) and indi-

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Table 2: Systematic list of the bat species of the La Gamba region (Piedras Blanca National Park, Costa Rica). Total number of individuals sampled during 59 trapping nights from 2.1.-26.3.1997 and from 17.1.-26.3.2004 for the entire area and for the main habitats: P = primary forest; S = forest margins / secondary forest; SW = sampling sites at the border of the National park, SE = data from two sites approx. 1.5 km east to the NP (only sampled 2004); C = cultivated semi-open land; G = gallery woodland and other forested corridor sites (sampled 1997) in the open landscape to the east of the NP. Species are assigned to the following foraging guilds: IA = insectivorous (aerial), IG = insectivorous (gleaning); N = nectarivorous (gleaning); FU = frugivorous (understorey gleaning); FC = frugivorous (canopy gleaning); G (gleaners: O = omni- to carnivorous, S = sanguinivorous).

Species (Family)	common name	Guild	**1997**	**2004**	**P 97**	**P 04**	**SW 97**	**SW 04**	**SE 04**	**C 97**	**C 04**	**G 97**	**G 04**
Emballonuridae													
Centronycteris centralis	Shaggy Bat	IA	1	1	1	1							
Rhynchonycteris naso [2]	Proboscis Bat	IA	4	10		3	3	2		1		1	5
Saccopteryx bilineata [2]	Greater White-lined Bat	IA	13	14	1		2	8		6	6	4	
Noctilionidae													
Noctilio albiventris	Lesser Fishing Bat	IA	-	11							9		2
Mormoopidae													
Pteronotus gymnonotus	Big Naked-backed Bat	IA	1	-	1								
Pteronotus parnellii	Common Mustached Bat	IA	60	26	18	6	11	2		3	2	28	16
Phyllostomidae													
- Phyllostominae													
Micronycteris hirsuta	Hairy Big-eared Bat	IG	13	1	13	1							
Micronycteris microtis	Common Big-eared Bat	IG	6	1	3		3	1					
Micronycteris nicefori	Niceforo´s Big-eared Bat	IG	4	-	3		1						
Micronycteris schmidtorum	Schmidt´s Big-eared Bat	IG	7	-	5		2						
Phyllostomus discolor	Pale Spear-nosed Bat	GO	9	9		1	9	4					4
Phyllostomus hastatus [1]	Greater Spear-nosed bat	GO	2	2	1		1						2
Tonatia brasiliense	Pygmy Round-eared Bat	IG	2	3		1	2	1	1				
Tonatia saurophila	Pygmy Round-eared Bat	IG	17	-	14		3						
Trachops cirrhosus	Fringe-lipped Bat	GO	3	-			3						
Vampyrum spectrum	Great false vampire Bat	GO	2	-	2								
- Desmodontinae													
Desmodus rotundus [1]	Common Vampire Bat	GS	35	26	1	16	16	7	1		2	18	
- Carolliinae													
Carollia brevicauda	Silky Short-tailed Bat	FU	40 [4]	32	25[4]	11	12	11	9		1	3	
Carollia castanea	Chestnut Short-tailed Bat	FU	166[4]	125[4]	26[4]	30	138[4]	56[4]	20		5	2	14
Carollia perspicillata	Seba´s Short-tailed Bat	FU	181[4]	100[4]	30[4]	34	121[4]	44[4]	5		14	30	3
- **Glossophaginae**													
Anoura cultrata [3]	Handleys Hairy-legged B	N	6	-	6								
Anoura geoffroyi	Geoffroy´s Hairy-legged B	N	-	2		2							
Choeroniscus godmani	Godman´s Whiskered Bat	N	-	1					1				
Glossophaga leachii [3]	Gray´s Long-tongued Bat	N	-	1		1							
Gloss. commissarisi	Brwon Long-tongued Bat	N	10	2	1	1	6		1			3	
Glossophaga soricina	Common Long-tongued B	N	11	3		2[4]	4		1			7	
Hylonycteris underwoodi	Underwoods Long-tongued Bat	N	-	3		3							
Lichonycteris obscura	Dark Long-tongued Bat	N	1	1				1				1	
- Lonchophyllinae													
Lonchophylla robusta [1]	Orange Nectar Bat	N	6	6	2		3	2	1			1	3
Lonchophylla mordax	Goldman´s Nectar Bat	N	25	15	10	10	14	4	1			1	
- Stenodermatinae													
Artibeus jamaicensis	Jamaican Fruit-eating Bat	FC	62	68	7	6	8	21		2	12	45	29
Artibeus lituratus	Great Fruit-eating Bat	FC	17	19	9	4	4	4			3	4	8
Artibeus phaeotis	Pygmy Fruit-eating Bat	FC	46	15[4]	19	7	24	5	1			3	2
Artibeus watsoni	Thomas´ Fruit-eating Bat	FC	75	112[4]	37	38	28	44[4]	16	2	6	8	8
Centurio senex	Wrinkle-faced Bat	FC	-	2		2							
Chiroderma villosum	Hairy Big-eyed Bat	FC	4	-	3							1	
Platyrrhinus helleri	Hellers Broad-nosed Bat	FC	11	15	1		1	8	2		2	9	3
Sturnira lilium	Little yellow-shouldered Bat	FC	27	41	1		9	13		2	11	11	17
Sturnira mordax	Talamancan -"-. Bat	FC	-	1									1
Uroderma bilobatum	Common Tent-making B	FC	28	49	1		11	19	1	1	12	16	17
Vampyressa nymphaea	Striped Yellow-eared Bat	FC	-	7		2			5				
Vampyressa pusilla	Little Yellow-eared Bat	FC	17	10	15	7		2	1			2	
Vampyrodes caraccioli	Great Stripe-faced Bat	FC	1	4	1			3					1
Thyropteridae													
Thyroptera tricolor	Spix´s Disk-winged Bat	IA	-	1									1

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Table 2: continued

Species (Family)	common name	Guild	1997	2004	P 97	P 04	SW 97	SW 04	SE 04	C 97	C 04	G 97	G 04
Vespertilionidae													
Rhogeessa io [3]	Rainforest Yellow Bat	IA	-	2							2		
Rhogeessa tumida	Centr.American Yellow B	IA	3	2			2	2				1	
Myotis nigricans	Black Myotis	IA	8[5]	20[4]	7	16[4]	1				3		1
Myotis riparius 3	Riparian Myotis	IA	-	5		5							
Eptesicus furinalis	Argentine Brown Bat	IA	-	2				2					
unidentified family /genus	(escapes from net)			(12)		(4)		(4)			(4)		
captured individuals			922	782	264	214	442	270	67	17	94	199	137
species numbers			37	41	30	25	28	24	16	7	15	22	19

[1] species also recorded at a roosting cave within mature forest approx. 3 km NE of the field station
[2] species also commonly found at roosts & nursery sites at Esquinas Rainforest lodge and the La Gamba field station.
[3] identification of species slightly uncertain (preliminary finding)
[4] sample includes 1-2 specimens of the genus with uncertain species assignment
[5] eight individuals of *Myotis* sp. (not identified to species) assigned to this species

viduals were then secured and kept in a cotton bag for identification and detailed morphometric treatment. This was done later the same night at a nearby station with good working (and light) conditions. Bats were identified to species (using the keys of REID 1997, TIMM & LAVAL 1998 , LAVAL & RODRIGUEZ 2002), weighed and at least 5 external morphological characters were measured on each bat (length of body, forearm length, tibia length, tail length and ear length). Animals were released after treatment. In March 2004, bats were individually marked before release with a pinhole code (patagium punching) in order to get information about local movements.

Data analysis

In order to improve sample size and to complete species lists, we pooled data of all sampling sites for the main habitat types and we also pooled the more recent data from 2004 with that collected 1997 at the same areas in nearby locations.

For comparisons of local communities each bat species was assigned to one of six raw foraging guilds: N = nectarivore, FC = frugivore – mostly canopy gleaning, FU = frugivore – mostly understorey gleaning (including some partly insectivorous species), IA = insectivore – aerial and IG = insectivore – gleaning. Omnivore gleaners and some specialised species (piscivore/sanguivores) were grouped together in a "gleaner guild" (OG). Assignments were based on information in HUMPHREY et al. 1983, REID 1997, LAVAL & RODRIGUEZ 2002, GIANNINI & KALKO 2004). Differences in the guild structures of the main habitats were assessed by comparing dominance patterns of individuals belonging to the distinguished foraging guilds via simple chi-squared tests. Differences in capture heights were tested with two-sided *t*-tests after assessing levels of variance. We give Shannon's diversity index for the bat assemblages of each habitat sampled, although we feel that such indices should be interpreted with great care for inter-habitat comparisons for the following reasons: (1) sampling effort is not equal between different sites and periods, (2) even when sampling effort is equal between different sites, the use of diversity indices may be problematic especially because the presence or absence of rare species, which often occurs just by chance, may affect the outcome of diversity indices (see STONER 2005). We therefore mainly rely on simple rank-abundance graphs to make initial comparisons between the bat communities of primary and secondary habitats in our investigation area and give a simple dominance index (after MC NAUGHTON: $100 \times y_1+y_2/Y$) were the abundance of the two dominant species (y_1+y_2) is related to the entire sample size (number of all individuals of all species Y).

Results

Species composition and general abundance patterns

Altogether, about 49 bat species belonging to 6 families were recorded in the La Gamba region in 1997 and 2004. Eight species reported in 1997 were not found in 2004 and 12 species captured in 2004 are lacking in the 1997 data set (Table 2). The local occurrence of one or two species is slightly uncertain because only 1 to 2 individuals were captured and some doubts remain about the determination (Table 2, see discussion). Secure identification to species level was also not possible for a few individuals of the genera *Carollia, Artibeus* and *Myotis*, and such individuals have been assigned to the most likely (or abundant) species in the overview in Table 2. The species and family list in Table 2 is supplemented with assignments of each species to one of six general foraging guilds and with the number of individuals captured in the main habitats during the two inves-

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Fig. 3: The sanguivore *Desmodus rotundus* (**a**) was captured at different habitats in the La Gamba region: from near roosting sites in pristine ridge forests (site P1 = (**b**), to "stepping stone"-habitats at forest edges (abandoned cocoa plantation: site S2 = (**c**), to its foraging grounds (cattle pasture C1 – (**d**). Photos: A. Vorauer.

tigation periods (1997, 2004), allowing a first assessment of species-specific local abundances.

A total of 1702 individuals was captured. Of this total, 12 individuals escaped from nets before an assignment to genus or even family level was possible (but these data are used for the calculation of capture efficiency; see Tables 1 & 2). Members of the family Phyllostomidae were dominant in the La Gamba bat community. Overall, this family contributed 76% of species and 88% of all individuals sampled (37 species, 1495 individuals). These 37 species belong to 6 different subfamilies whose members show pronounced differences in local species diversity, abundance and foraging strategies. Whereas the mainly canopy-gleaning frugivorous subfamily Stenodermatinae (e.g. Fig. 4d) was the most species-rich group (13 species; 41% of all captured phyllostomid bats), understorey frugivores (subfamily Carolliinae) were dominant in terms of abundance, about 43% of all phyllostomid bats (and 38% of all bats captured) belonging to only three *Carollia* species (e.g. Fig. 4e). Members of the subfamily Phyllostominae (e.g. Fig. 4b), which are mostly insectivorous or omni- to carnivorous gleaners at lower strata, are species rich in the area (10 species), but in both investigation years have only been recorded at low densities (together 5.4% of all phyllostomid bats). This is also true for the 10 nectarivore species (e.g. Fig. 4f) of the closely related subfamilies Glossophaginae and Lonchophyllinae (6.2%), from which only one species, *Lonchophylla mordax*, has been recorded in both years in substantial numbers. It should be stated however, that some species of this group are not easily distinguishable under field conditions (e.g. *Anoura* spp.) and that the assignments of captured individuals to particular species may not be correct in all cases (which is also true for some Vespertilionidae, cf. Table 2).

The sanguivore Common Vampire Bat (*Desmodus rotundus*, Desmodontinae, Fig. 3a) seems to be quite common around La Gamba and was not only captured at or near cattle pastures but was also found at forest edges with small creeks, at the edge of the primary forest and even within mature forests (roosting caves) at quite a distance from the forest margins. All 12 species from the remaining 5 families (see Table 2) are aerial insectivores (e.g. Fig. 4c) and may thus be under-represented in the

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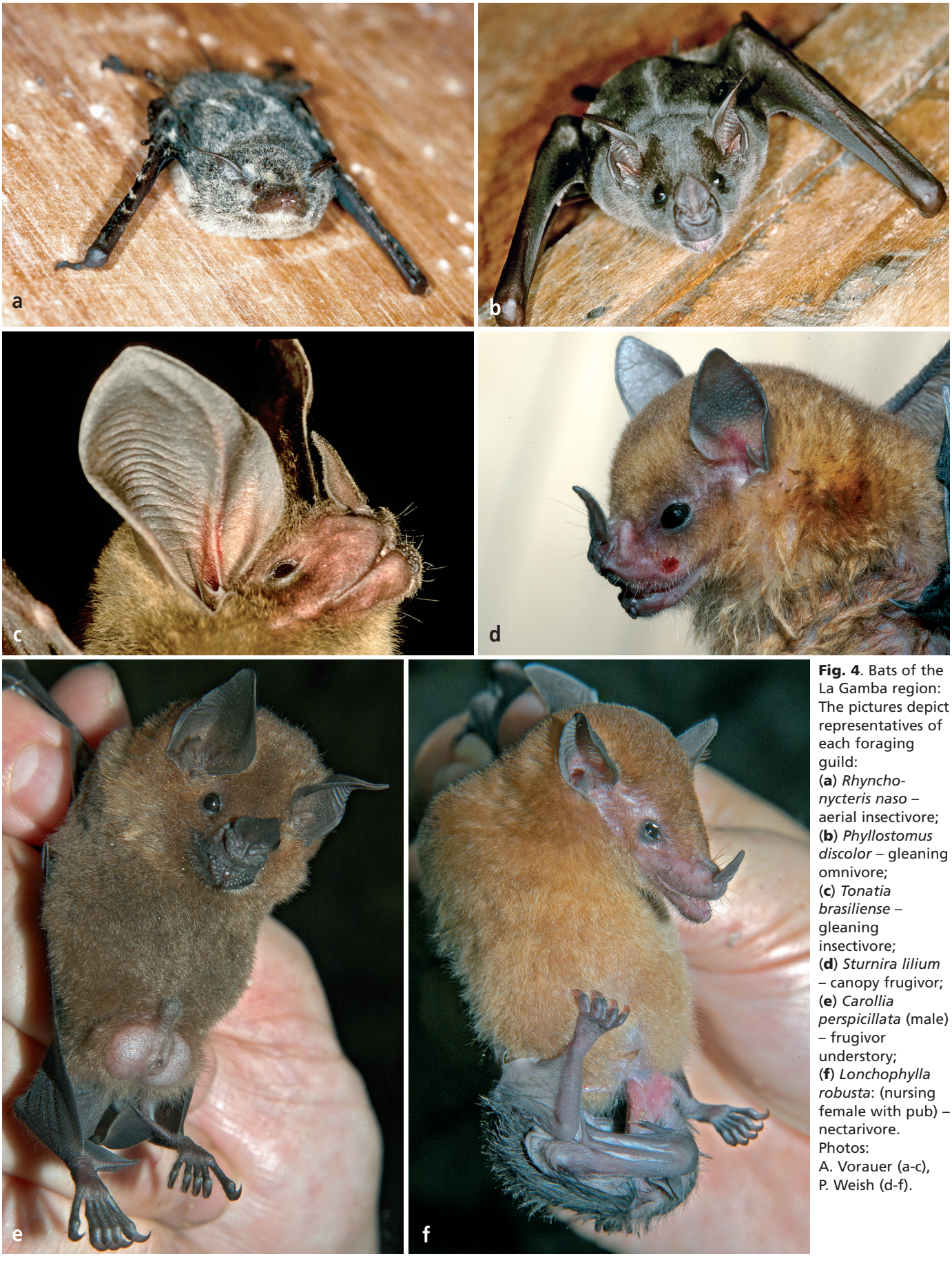

Fig. 4. Bats of the La Gamba region: The pictures depict representatives of each foraging guild: (**a**) *Rhynchonycteris naso* – aerial insectivore; (**b**) *Phyllostomus discolor* – gleaning omnivore; (**c**) *Tonatia brasiliense* – gleaning insectivore; (**d**) *Sturnira lilium* – canopy frugivor; (**e**) *Carollia perspicillata* (male) – frugivor understory; (**f**) *Lonchophylla robusta*: (nursing female with pub) – nectarivore. Photos: A. Vorauer (a-c), P. Weish (d-f).

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Table 3: Relative importance of foraging guilds in bat assemblages of different habitats around La Gamba: S = species / guild; I = individuals / guild; D% = guild dominance. Pooled data for forest margins at both sides of the La Gamba region (see SW+SE in Table 2).

	Total	Primary forest			Secondary forest			Cultivated land			Corridors		
Guild	D%	S	I	D%	S	I	D%	S	I	D%	S	I	D%
FU	38.1	3	156	32.9	3	416	53.7	3	20	18.7	3	52	15.5
FC	37.1	12	160	33.7	9	230	29.7	6	53	49.5	11	185	55.0
IA	10.9	7	59	12.5	6	35	4.5	6	32	29.9	7	59	17.6
IG	3.2	6	40	8.4	5	14	1.8	0	0	0	0	0	0
N	5.5	8	38	8.0	6	39	5.0	0	0	0	5	16	4.8
GO	5.2	4	21	4.5	4	41	5.3	1	2	1.9	3	24	7.1
total	100	40	474	100	34	775	100	16	107	100	29	336	100

mist net samples. Accordingly, only three species of this guild reach a dominance level of about 1% and according to the data, only *Pteronotus parnellii* can be regarded as common in different habitats of the area. It was abundant especially at one corridor site, which might have been located close to a roosting site of this species. The mainly insectivore and occasionally piscivore Lesser Fishing Bat (*Noctilio albiventris*, Noctilionidae), a species foraging low over ground, has been caught only in the late dry season 2004 (mid March) at running water in the open landscape in the La Gamba valley and may be more common in the area than suggested by our data.

Bat community structures in different habitats

Species numbers, species composition, dominance and guild structures, as well as relative abundances (bat densities expressed over capture rates) showed pronounced differences between the main habitats around La Gamba (Tables 1-3, Fig. 5).

The primary forest sites together yielded 40 bat species. While only nine species of the La Gamba region (so far) were not recorded in mature forest habitats, 10 species were found exclusively at such sites. However, of this high total only a third has been caught in larger numbers and at more than one to three sample sites. The number of rare species is reflected by the length of the "tail" in the rank abundance graph (Fig. 5), indicating the high number of species (19) of which only one or two individuals were sampled (see also Table 2). Also, all species exclusively found in the primary forest seem to be rare even there, the Hairy Big-eared Bat (*Micronycteris hirsuta*) being the only species of this group which has been caught (albeit only in 1997) in some numbers. Thus, although the primary forest shows a high value for species diversity (Shannon index), the dominance curve is somewhat unbalanced, with the five most abundant species accounting for 55% of all individuals and with a comparatively high dominance index (29%). In addition, bat densities as expressed over capture rates were significantly lower at most mature forest sites than at forest margins near the primary forest and at gallery woodland and other corridor habitats (Table 1).

Secondary forests were sampled with similar intensity to primary forest sites (Table 1). Although species numbers and species diversity values were clearly lower in this habitat type (32 species near the national park plus two species found only at the opposite side of the La Gamba valley), when all data from both investigation years are pooled, altered forests still represent an important and species-rich habitat for bats. In 2004, for instance, we found no difference in the number of bats sampled per night between primary and secondary forest sites. Furthermore, both the 1997 data and the 2004 data indicate much higher bat densities in secondary forests than in primary forests. However, the high densities are mainly the outcome of the dominance of only three generalistic phyllostomid frugivores (*Carollia castanea*, *C. perspicillata*, *Artibeus watsoni*: Table 2) which is also expressed in high dominance indices of the forest margin communities (Fig. 5). Also, species numbers at secondary forest sites were twice as high near the national park than at isolated sites across the La Gamba valley (16 species). Nevertheless, this may be simply an artefact of the lower sampling effort at these sites, and the dominant species did not differ between both subsets of secondary forest sites.

Despite much less capture effort in gallery woodland and other forested corridors, these habitats showed nearly the same species richness and slightly higher capture rates than secondary forest sites. Moreover, when species diversity and dominance values, and (in part) guild patterns, are considered, these sites were more similar to primary forest than to the secondary forests (Fig. 5, Table 2-3).

Because six species were caught in comparatively high (and similar) numbers and because the species list is short with only a few "rare" species, the open to semi-open cultivated habitats showed the lowest dominance index and reached a comparatively high species diversity index.

Although most species which were captured at disturbed secondary habitats were also found in our primary forest sites, there are at least five species belonging to different foraging guilds (*Saccopteryx bilineata*, *Phyl-*

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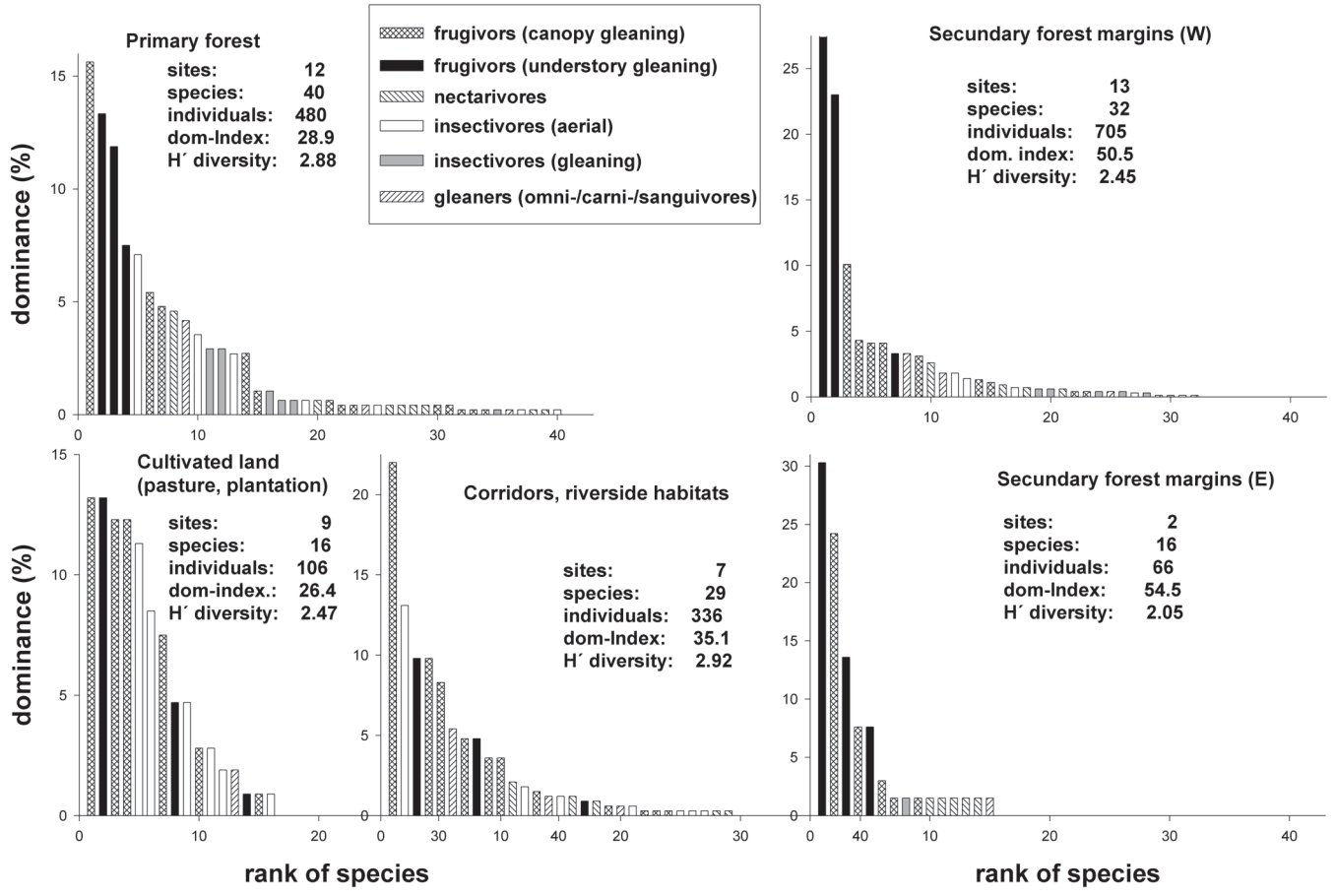

Fig. 5. Rank-abundance (dominance-diversity) graph of bat species belonging to six foraging guilds at different habitats in the La Gamba-area 1997 and 2004. Secondary forest habitats: W = near the Piedras Blancas NP, E = across the La Gamba valley. Details see Text.

lostomus discolor, Platyrrhinus helleri, Sturnira lilium, Uroderma bilobatum) which seem to thrive much better in the altered or cultivated landscape than in the primary habitats of the Esquinas forest. These species were only captured once at a single P-site, but were regularly captured at different disturbed sites in higher numbers (see Table 2). In addition, *Noctilio albiventris* was only found in the open landscape of the La Gamba valley along the Rio Gamba and along a little creek at a nearby cattle pasture (sites G1, C2).

Guild structures

The relative composition of the distinguished foraging guilds differed significantly between all main habitats ($p < 0.001$, χ^2 tests with 5 degrees of freedom (d.f.) for comparisons of habitats: P vs. S, C & G; S vs. C & G, and $p < 0.01$ for C vs. G, 4 d.f.; Table 3). Six foraging guilds were observed at the primary and secondary forest sites, whereas only five and four were observed at the gallery woodland (corridor) and cultivated landscape sites, respectively. When all individuals within a specific guild were treated as if belonging to one "guild species", foraging guild diversity (Shannon index) was highest at primary forest sites (H´= 1.54), lowest at cultivated sites (H´= 1.1) an intermediate at secondary forest margins (1.21) and gallery woodlands (1.26).

Although the two most highly represented foraging guilds at all habitat types were understorey and canopy gleaning frugivores, there were pronounced differences between habitats in the species diversity within the FC guild (Table 3) and in the dominance ranks of the frugivorous species. Whereas the mainly canopy gleaning species of the subfamily Stenodermatinae made up about one third of total captures in the forested sites, this guild (with fewer species) made up about 50% of all captures in the open cultivated landscape (gallery woodland, pastures). On the contrary, understorey gleaning frugivores (*Carollia* spp.) were much more dominant in primary and especially in secondary forest habitats than in more open corridor habitats and pastures. Also, insectivorous to carnivorous gleaning species of the subfamily Phyllostominae showed a clear preference for forested sites, although gleaning omnivores contributed less than 10% to the total captures in all investigated habitats around La Gamba (Table 3). Aerial insectivores on the other hand, with 6-7 species made up a comparatively high proportion of total cap-

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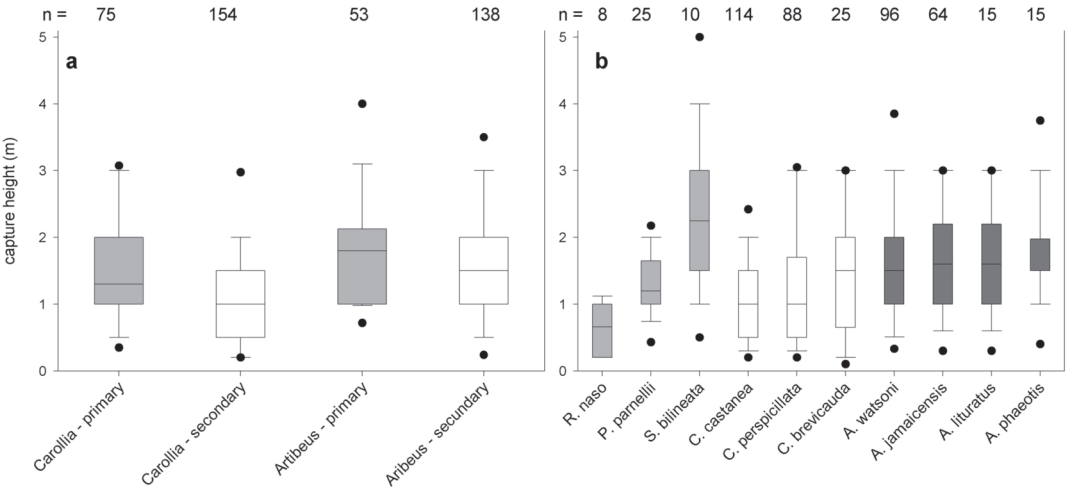

Fig. 6: Niche segregation within ecological guilds as indicated by different capture heights of bats in the La Gamba region: (**a**): Capture heights of 3 *Carollia* and 4 *Artibeus* species in primary and secondary habitats respectively. (**b**): Capture heights of different species of aerial insectivores (left), understorey frugivores (middle) and canopy frugivores (right). Box plot charts displaying the median, 10th, 25th, 75th and 90th percentiles with outliers (5 & 95% percentiles).

tures in the cultivated landscape whereas gleaning insectivores were absent there. This latter guild (with 6 species) and nectarivores (8 species) were only significant in the mature forest.

Niche segregation within foraging guilds

We used the capture heights of individual bats in our mist net samples from 2004 (net heights up to 4.5 m) in order to test whether species-specific differences in the use of "air bands" exist between species within single foraging guilds and between habitats. We focus here on three groups of species with larger capture rates: aerial insectivores of the families Emballonuridae and Mormoopidae, and two groups of congeneric frugivores, the understorey gleaning Carolliinae (*Carollia* species) and the more canopy gleaning Stenodermatinae (*Artibeus* species). Fig. 6a shows that on average *Carollia* and *Artibeus* species tended to be caught higher in mist nets at primary forest sites than at secondary forest sites. Differences were significant for *Carollia* spp. (P: 147 ± 88 cm vs. S: 109 ± 84 cm; $t = 3.16$, $p < 0.01$) but not for *Artibeus* (P: 187 ± 97 cm vs. S: 165 ± 96 cm; $t=1.41$, ns), but were significant between the two frugivorous groups (*Carollia* vs. *Artibeus*) both in primary forest ($t = 2.42$, $p < 0.05$) and in secondary habitats ($t= 5.31$; $p < 0.001$). So, as could be expected, canopy gleaners were caught higher in the nets than understorey gleaners, which is also the case when single species of both guilds are compared (Fig. 6b).

In Figure 6b, we pooled data from different forested sites in order to compare capture heights between single species within the different guilds. There were no strong differences between species within the two frugivorous guilds. However, in both guilds, the differences between the average capture heights of the lowest and highest flying species (*Carollia castanea* 108 cm vs. *C. brevicauda* 145 cm; *Artibeus watsoni:* 166 cm vs. *A. phaeotis* 200 cm) may indicate some differences in foraging strategies, although only capture heights between *C. castanea* and *C. brevicauda* ($t= 2.21$; $p < 0.05$) differed significantly. There were no significant differences between *C. perspicillata* and *C. brevicauda* and no differences between any of the *Artibeus* species.

Segregation in average flight (capture) heights was more pronounced in aerial insectivores. Despite the comparatively small sample sizes for species of this guild there were significant differences in the average capture heights between all three species of the guild. The average capture height of the two "Sac-winged Bats" *Rhynchonycteris naso* and *Saccopteryx bilineata* differed by 1.7 m, *R. naso* being caught very low above ground, (66 ± 43 cm), and *S. bilineata* mostly above 1.5 m (235 ± 124 cm; $t = 4.01$; $p < 0.01$). The mormoopid *Pteronotus parnellii* was caught at intermediate heights (125 ± 53 cm), but significantly higher than *R. naso* ($t= 3.18$; $p < 0.01$) and lower than *S. bilineata* ($t = 2.70$; $p < 0.05$).

Discussion

Bat diversity of the Piedras Blancas National Park area

There are at least 108 species of bats belonging to nine families in Costa Rica (LAVAL & RODRIGUEZ 2002). Given its small size, Costa Rica may thus be regarded as one of the countries with the greatest species diversity of bats. Within Costa Rica, there is a gradient of decreasing species diversity from the lowlands to higher elevations, and a decrease in species numbers may also be expected from the south to the north with increasing distance from the equatorial zone. Given this background, our investigation area at the southernmost lowland area of Costa Rica which also encompasses a wide variety of environmental conditions and harbours some of the most species-rich life zones in Costa Rica

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(POWELL & BARBORAK 2000, WEISSENHOFER et al. 2001, SÁNCHEZ-AZOFEIFA et al. 2003), could be expected to be one of the bat "hot spots" not only in Costa Rica, but in the whole of Central America. We feel that these expectations are fulfilled by our results. According to JANZEN (1983), 145 of the 200 Costa Rican mammal species, including 80 bat species, have been detected or are expected to occur in either Osa or Golfo Dulce region. According to distribution maps and data summarised by REID (1997) and LAVAL & RODRIGUEZ (2002), this figure drops to about 70 species (or 65% of the total Costa Rica bat fauna), if one refers only to lowland species which mainly or exclusively occur, below about 600 m altitude. Although identification of some species is still somewhat uncertain (see below) with about 50 species from six families, the Piedras Blancas National Park area can be regarded as extremely species rich (about 45% of all Costa Rican bats and about 70% of all possible species of the Golfo Dulce region). In the course of our investigations, bats were only sampled by ground level mist nets, but neither canopy netting nor acoustic monitoring took place. These limitations in methodology mean that our species list is likely to be incomplete and biased (cf. VOSS & EMMONS 1996, LIM & ENGSTROM 2001, KALKO 1997, 1998, SAMPAIO et al. 2003). Presumably only the fraction of species occupying the lower strata is well represented. In particular, most aerial insectivores will be under-represented because many species of this group forage at higher strata or above the forest canopy, and, in addition, tend to avoid mist nets due to their well developed echolocation systems. In our data, this bias is not only visible by the low capture rates of aerial insectivores, which, despite comprising a quarter of all species, only account for 10.7% of captures, but also by the disproportionately high number of 13-14 aerial insectivores which are expected to occur in the region but are missing in our sample. Members of the family Molossidae are totally absent (4 further species possible), and only a few Emballonuridae (4-5 further species possible) and Vespertilionidae species (3 further species possible) are listed (Table 2). We therefore conclude that the already high overall species diversity of the Esquinas forest is (much?) higher than recorded so far. This is also true for the local species diversity of the La Gamba region. With regard to the stated methodological limitations, the comparatively low sampling effort with only late dry season sampling, and with respect to the very restricted, small sampling area (only about 6 km²), our investigation area possibly has one of the highest values of alpha diversity reported so far from neotropical lowlands. Although the number of localities with reasonably complete species lists is still limited, for the majority of such (mostly much larger) sites, inventories indicate between 35 and 65 (exceptionally 20-75) species (see VOSS & EMMONS 1996, SORIANO 2000, STONER 2005 with further references). In Costa Rica, for instance, the bat lists of even the best investigated areas, i.e. La Selva and Palo Verde, comprise no more than 67-68 species for the entire national park areas (TIMM 1994, STONER & TIMM 2004).

As in most other neotropical areas (e.g. STONER 2005), members of the family Phyllostomidae were highly dominant in the La Gamba bat community. If only this most diverse bat family, whose members can be recorded more appropriately with the aid of ground level mist nets, is considered, the tiny La Gamba region contains more species (37) than Palo Verde (32) and only a slightly fewer than La Selva (42). Overall, these comparisons clearly indicate that the bat fauna around the "Rainforest of the Austrians" mirrors the outstanding diversity of its flora and vegetation (e.g. WEISSENHOFER et al. 2001) and of other organisms (see several contributions in this book). Our bat data therefore should be regarded as an additional argument for increased future habitat conservation efforts in the region.

Status of local species with regard to the situation in Costa Rica

The above point of view is further emphasised by the Costa Rican distribution and conservation status of the locally occurring bat species. According to the assessments in LAVAL & RODRIGUEZ (2002), many of the bat species so far recorded around La Gamba are stated as "uncommon" if not "rare" in Costa Rica. Fourteen out of the 49 species listed in Table 2 are widespread and abundant to common throughout Costa Rica, at least in wetter parts of the lowlands. This quarter of species accounts for 58% of all captures and includes most of the species with higher dominance ranks (> 3% or more than 50 individuals) in our sample. Another eight species, including the locally abundant *Artibeus watsoni* and *Sturnira lilium* are stated to be at least "locally common" in Costa Rica by LAVAL & RODRIGUEZ (2002). Most of the 16 "uncommon" Costa Rican lowland species were only recorded in small numbers also at La Gamba (14% of total captures). Nevertheless, some of these species (namely *Lonchophylla mordax*, *Platyrrhinus helleri*, *Uroderma bilobatum*, *Vampyressa pusilla*) were captured in comparatively large numbers and at more than one site and habitat in our investigation, which might indicate healthy local populations. This may also be true for some more specialised forest dwellers like *Micronycteris hirsuta, Tonatia saurophila* or *Glossophaga commissarisii* (cf. Table 2). Finally, about ten species which are known from only a few sites in Costa Rica and are stated as "rare" or "very rare" by LAVAL &RODRIGUEZ (2002) (or could not be expected at Pacific lowland sites), were recorded in low num-

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bers (total: 36 individuals). Most of these species were captured at or only near primary forest sites: *Centonycteris centralis*, *Miconycteris nicefori*, *M. schmidtorum*, *Glossophaga leachii*, *Hylonycteris underwoodii*, *Centurio senex*. In contrast, the rare Dark long-tongued Bat *Lichonycteris obscura*, so far reported only from very few dense forest localities in Costa Rica (Caribbean Lowlands and San Jose area) was captured in both investigation years at disturbed forested habitats and *Choeroniscus godmani* only once at the margin of a secondary forest across the La Gamba valley (S5).

A few identifications of such rare species still remain somewhat doubtful (distinctions between the two *Anoura* species, *Rhogeessa* and *Myotis* spp.) or require further confirmation. Also, the status of *Micronycteris nicefori*, a species which in Costa Rica so far was thought to be restricted to Caribbean and northern lowlands, and of the highland species *Sturnira mordax*, which is mainly known from the Caribbean slope (but also occurs on the south-western Pacific slope) needs to be clarified. The latter species was captured only once in March 2004 in the gallery woodland along the La Gamba river, and was possibly a transient individual.

Community composition in different habitats

Although the four different main habitats sampled in our study were close to each other, our results, as visualised by rank-abundance graphs, clearly indicate pronounced differences in species richness, species composition and dominance patterns between these habitats. Not surprisingly, the mature primary forest showed highest species numbers and a more even distribution of species over the abundance ranks. For instance, the most abundant species at primary forest sites (*Artibeus watsoni*: 15.6% of total numbers) was only twice as abundant as the most abundant aerial insectivorous species (*Pteronotus parnellii:* rank 5) and only five times more abundant than the first gleaning insectivorous species (*Tonatia saurophila:* rank 11). At nearby secondary forest sites, which are nonetheless species rich (32 species recorded), species abundance patterns were much more uneven, with the two dominant species *Carollia castanea* (27.5%) & *C. perspicillata* (23.5%) contributing more than 50% of all captures and the rank 5 species (*Artibeus phaeotis*) being nearly 7 times and the highest ranking insectivorous species (*Pteronotus parnellii*: rank 11) 15 times less abundant than *Carollia castanea*. Such differences probably reflect mainly a lower diversity of horizontal and vertical vegetation structures, of floral richness (cf. WEISSENHOFER et al. 2001) and of food resources at the disturbed secondary forest sites. Although these data once more emphasise the outstanding value of tropical rainforests for maintaining a diverse bat fauna (see for example FENTON et al 1992, MEDELLIN et al 2000, BERNARD & BROCK-FENTON 2002), they still may underestimate the real importance of these mature forest stands for local ecosystem functions on a landscape scale. Several studies have demonstrated that semi-natural structures (like secondary forest patches, plantations, remnants of woodland at rivers and pastures) in disturbed landscapes are of high conservation value and show surprisingly high species numbers of vertebrates (e.g. DAILY et al 2003, LUCK & DAILY 2003, ESTRADA & COATES ESTRADA 2001, 2001a). Nevertheless, the comparatively high diversity and especially the high densities of bats in such disturbed semi-open to open habitats around La Gamba in our opinion are at least partly a result of the vicinity to the pristine Esquinas forest. Because of their dispersal abilities many species which still rely on mature forests (e.g. by using the great variety of day roosts in undisturbed areas), should be able to use adjoining habitats and to fulfil their important ecological services there.

It is remarkable that the most abundant species in the cultivated landscape and especially along corridors (*Artibeus jamaicensis*, *A. watsoni*, *Carollia perspicillata*, *Pteronotus parnellii*, *Sturnira lilium*, *Uroderma bilobatum*) are known to be wide ranging and/or represent the largest members within their guild or genus. In fact, we have scant direct data from marked individuals which prove that some species range widely within our investigation area and disperse from primary forests in the national park out into the disturbed landscape of the La Gamba valley. For instance, single males of *A. jamaicensis* and of *Uroderma bilobatum* originally captured at the S2 site (near the primary forest) crossed the open valley and were recaptured about 2 km away along the La Gamba river (site G2), and one female *Carollia castanea* captured near the edge of the primary forest (C1) was recaptured one day later across the valley at site S5, and a male *C. brevicauda* captured at the ridge forest (P1) was found at the edge of a secondary forest on the opposite side of the valley (S4) the next day.

In addition, some dominant species at disturbed habitats are reported to have generalised habitat requirements (e.g. *P. parnellii* — see FLEMING et al. 1972) and/or benefit from the presence and high concentrations of their preferred food (or roost) plants like *Ficus*, *Piper*, *Solanum*, and *Musa* at forest margins, along live fences and at the edges of gallery woodland. This is especially true for *Piper* specialists such as *Carollia*, and *Solanum* specialists like *Sturnira* (compare ESTRADA & COATES ESTRADA 2001 with similar results from disturbed landscape in Las Tuxtlas, Mexico). Nectarivorous species were generally captured in only low numbers in the La Gamba region. Nevertheless, the few species which were also caught in some numbers outside

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or at some distance from primary forest habitats (*Glossophaga soricina, Lonchophylla robusta*) are either habitat generalists (*G. soricina*) or are supplementing their food with insects, fruit pulp or pollen. In addition, in *Lonchophylla robusta*, as TSCHAPKA (2004) has pointed out, large body mass provides an energy buffer that permits daily commuting flights between profitable foraging areas and a permanent roost, and in fact roosting caves of this species exist in mature forest near La Gamba. Similarly, we know of at least two roosting sites of the sanguivorous *Desmodus rotundus* located a few hundred metres inside mature forests. From such "refuges", this species obviously starts its search for food throughout the landscape. As the comparatively high capture rates along corridors in the La Gamba region suggest (see Table 2), the Common Vampire Bat also utilises tree stands and forest remnants in the open landscape as "stepping stones".

Overall our corridor site data show that such forested areas are not only fulfilling this function for many other species from all foraging guilds (29 species recorded in corridor habitats around La Gamba), but moreover clearly indicate that in deforested landscapes these areas are also valuable bat foraging habitats in their own right, as long as they are not too far from forest remnants (see similar results ESTRADA & COATES ESTRADA 2001, SCHULZE et al. 2000, and DAILY et al. 2003 with further references for other mammals).

Among the cultivated landscape sites, shaded plantations with higher vegetation complexity were much richer in bat captures and species than open pastures, and for these habitats, distances to mature forest were an additional factor influencing bat diversity. During two sample nights in 2004, we captured 14 bat species with very high capture rates in an abandoned cocoa plantation adjoining the primary forest (site S2) and 10 species in much lower density in an oil palm plantation in the middle of the valley (site C3, Table 1). The two open cattle pastures sampled in 2004 differed in the amount and density of trees and shrubby vegetation and in their distance from the mature forest. Whereas 12 bat species were recorded at the more densely vegetated site C1 close to the edge of the forest, only 9 species were captured in the more open centre of the valley at site C2. However, capture rates were low at both sites in 2004 and were very low at the same pasture sites in 1997 with only 4 species sampled (Table 1).

Overall our results clearly show that there is no substitute for native rainforest habitats in tropical landscapes. However, our findings also indicate that the conservation of bat diversity and bat-driven ecological processes in disturbed tropical countryside can be improved by relatively small measures, such as maintaining or replanting live fences and protecting gallery woodland and secondary forest patches within the cultivated landscape.

Niche segregation within foraging guilds

In general, resource diversity and abundances can be expected to be high in neotropical ecosystems for bats (which is expressed by the unsurpassed diversity of this group in the tropics), and in part seem to allow for broad overlaps in morphological and dietary space (e.g. WILLIG et al. 1993). However, the high number of coexisting species within specific foraging guilds should also foster finely tuned niche segregation patterns especially between similarly sized and/or closely related species (congeners). In fact, for some species (species groups) occurring in our investigation area, some studies have already demonstrated niche segregation at different levels. Phytophagous phyllostomids at Barro Colorado Island (Panama), for instance, separated into *Piper*-specialists, *Ficus*-specialists, and eclectic plant eaters which in turn were the main consumers of flower products (GIANNINI & KALKO 2004). On the same island, HUMPHREY et al. (1983) demonstrated niche segregation between surface gleaning omnivorous and insectivorous bats over food item size (fostered by interspecific differences in size of the dentary apparatus) and also documented differences in vertical and horizontal microhabitat use. That vertical stratification may account for additional spatial and resource partitioning in complex tropical bat communities has been already suggested by FLEMING et.al. (1972) and MCNAB (1971), and has been clearly documented in several studies, albeit mostly at broader spatial scales (i.e. capture rates at canopy vs. ground nets; e.g. LIM & ENGSTROM 2001, KALKO & HANDLEY 2001). In our sample, significant differences in capture frequencies of some of the better-sampled species in higher and lower fractions of our ground nets indicate vertical stratification even at smaller scales (total net heights < 5 m above ground) and may therefore be a useful hint towards existing niche segregation mechanisms. The use of different air strata, i.e. flight at different heights above ground, could be the outcome of complex species-specific ecomorphological and physiological affinities and constraints (e.g. MCKENZIE & ROLFE 1986, CROME & RICHARDS 1988), but possibly also reflect differences in diet and foraging strategies. As a disproportionate subset of our captures happened within the first two to three hours after dawn (and thus perhaps directly after individuals had left their roost), species-specific differences in roost site selection (e.g. roost height) are also likely to contribute to the reported patterns and may also in part explain differences in capture heights between primary and secondary forest sites.

Vertical stratification was most prominent between

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syntopic aerial insectivores and especially between the two rather small emballonurid species *S. bilineata* and *R. naso*. Clear vertical niche segregation between these two species has also been reported from Guyana (LIM & ENGSTROM 2001) where *R. naso* was classified as a "strict understory specialist", with 96% of its captures being within 3 m of ground level, whereas 60% of captures of *S. bilineata* were above this zone. *Pteronotus parnellii*, the third aerial insectivore in our sample also strongly preferred ground level habitats (90% of captures below 3 m) in Guyana, but this species is much larger than *R. naso* and *S. bilineata* (12-26 g vs. 3-6 g and 6-9 g respectively; REID 1997, own data) so that dietary overlap is unlikely. Vertical stratification was much less pronounced between congeners within two frugivorous guilds. However, vertical segregation was significant at least for *Carollia castanea* and *C. brevicauda*, two species which do overlap in size (11-16 g vs. 13-20 g, REID 1997, own data) and are both specialists on plants of the genus *Piper*, although early successional plant species are also eaten. Previous studies have shown that when coexisting, *Carollia* species tend to differ in the relative percentages of fruit species consumed (FLEMING 1991, THIES & KALKO 2004, LAVAL & RODRIGUEZ 2002). The small differences in capture heights in the La Gamba region may therefore also reflect dietary segregation between *Carollia* species (and to a lower extent presumably also between species within the genus *Artibeus*).

However, as KALKO & HANDLY (2001) have stressed, "as a result of the differential use of space among bats, alterations of forest structure are likely to result in changes in structure and function of local bat communities, but our limited knowledge of natural history and ecology of many species limits definition of changes". From the viewpoint of the conservation of local bat assemblages, this again means that the best conservation measure around the Esquinas forest will be simply to preserve as diverse a forest as possible, but these efforts should also include buffer habitats and secondary structures in the cultivated landscape (see LASKA 1997, HARVEY & HABER 1998).

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